Radiation and Extinction: Investigating Clade Dynamics in Deep Time

Determining the causes and drivers of evolutionary dynamics is central to our understanding of life on Earth. What factors shaped the modern biota? Why did some groups go extinct, whilst others survived and radiated? Why are some groups so much more diverse than others? What will happen to organisms as the Earth continues to warm up? Many of these questions have inspired scientists for centuries (Cuvier, 1825; Darwin, 1859; Simpson, 1944), with foundational work in developmental biology, comparative anatomy, palaeontology, and geology providing provocative hypotheses that still influence current research on organismal evolution. New sources of data, however, from recent advances in molecular biology, computing, and imaging, as well as increasingly sophisticated quantitative methods, have provided unprecedented ability to test these hypotheses rigorously.

George Gaylord Simpson (1944) set the groundwork for the application of statistics to macroevolution, and he championed the seamless transition from modern to fossil samples in exploring these themes, but he could not have foreseen the remarkable advances in the subsequent 70 years. Simpson was passionate about systematics, and yet he could not then have conceived of the revolution wrought by the application of cladistics and phylogenomics to the generation of huge phylogenetic trees (e.g., Bininda-Emonds et al., 1999; dos Reis et al., 2012; Jetz et al., 2012; Meredith et al., 2011; Wiens et al., 2010). He was also knowledgeable about stratigraphy, but equally he could not have imagined the orders-of-magnitude improvements to dating of the rock record and consequent refinements to calibration and dating of time trees that then permit meaningful calculations of rates of evolution across trees (e.g., Aze et al., 2011; Brown & Yang, 2011; Donoghue & Benton, 2007; Stadler, 2011; Yang & Rannala, 2006). Finally, he could not have imagined how advances in computing capacity and in numerical methods and algorithms, as well as the creation of massive multi-contributor databases (e.g., The Paleobiology Database, www.paleobiodb.org), would have brought powerful multivariate and iterative approaches to bear on the problems he felt were closest to his heart (e.g. Alfaro et al., 2009; Alroy, 1999; Harmon et al., 2010; Hunt, 2012; Jablonski, 2001; Jablonski & Chaloner, 1994; Losos, 2010). Despite some wobbles in the 1980s and 1990s, it is surely right that phylogenomicists and palaeontologists now share problems, data, and solutions. The result has been an

explosion of studies in recent years (Fig. 1) reconstructing rates and patterns of evolution, testing complex evolutionary models, and examining the effects of intrinsic and extrinsic drivers on biodiversity, with palaeontological, neontological, and genomic data sets. These studies demonstrate the importance of examining evolution across deep time scales, incorporating extinct taxa and encompassing many previous shifts in climate and environment, including those potentially analogous to the modern world (Bown et al., 1994; Finarelli & Goswami, 2013; Hunt, 2007; Jablonski, 2001; Slater et al., 2012; Zachos et al., 2001). Only by taking full advantage of the rich data available for past and present biotas can we hope to understand the processes that generate and shape organismal diversity.

In November 2014, a two-day symposium and workshop on "Radiations and Extinctions: Clade Dynamics in Deep Time" was held at the Linnean Society of London and Imperial College London, with the goal of bringing together a diverse array of researchers developing and applying methods for reconstructing deep-time macroevolutionary patterns in biodiversity, with a particular focus on analytical approaches that take advantage of the wealth of data available in the fossil record. Speakers detailed both methodology and application for a range of taxonomic groups, time intervals, and macroevolutionary themes corresponding to radiation, extinction, and clade dynamics in deep time. The first day of presentations and discussion was followed by a second day of workshops in which participants were shown how to apply these new methodologies to their own datasets. In this special volume, many of the contributors to this meeting present detailed descriptions of new methods, conduct critical review and analyses of existing approaches, and apply these approaches to fundamental questions on the evolution of the modern biota.

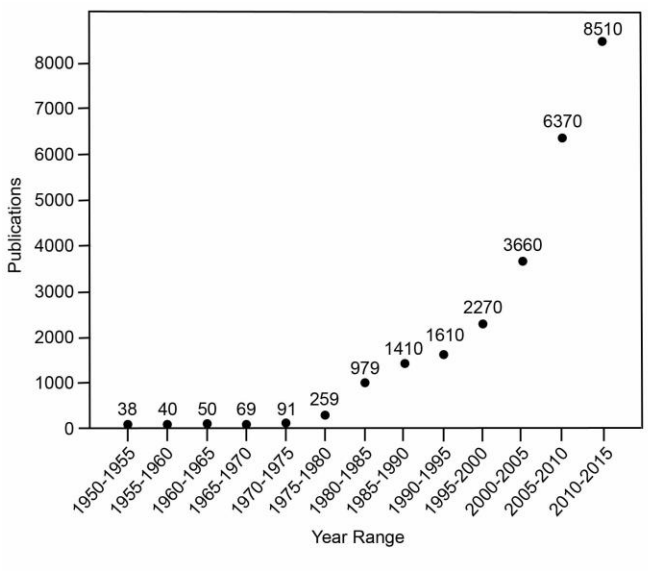

Figure 1. Publications relating to macroevolution, binned in 5-year intervals, as identified by Google Scholar.

Speciation and taxonomic diversity

Taxonomic diversity has been a cornerstone of macroevolutionary and macroecological research for decades, with highlights including Raup and Sepkoski's groundbreaking work on marine invertebrate diversity, which identified five mass extinctions in the Phanerozoic Eon (Raup & Sepkoski, 1982) and inspired a generation of researchers to investigate the validity, causes, and effects of these phenomena across diverse clades (e.g. Halliday & Goswami's [2016] study in this volume on the effects of the Cretaceous-Palaeogene mass extinction on mammal disparity). Taxonomic diversity is the product of the generation of new species and the loss of existing species, and isolating these attributes and understanding the factors that cause variations in them is fundamental to reconstructing the evolution of diversity. In this volume, Rabosky (2016) examines the causes of variation in rates of speciation. In generating biodiversity, the balance between speciation and extinction is key, and high rates of speciation characterize many so-called 'explosive' radiations, such as cichlid fishes or Paleogene mammals. In particular he discusses why speciation rates are so variable across the tree of life, with sister clades often exhibiting hugely different modern diversities (e.g. compare monotremes and therian mammals, or holostean and teleost fishes, or crocodylians and birds). He points out that perhaps too much research has focused on reproductive isolation, all the barriers to gene pool mixing that emerge during the process

of species formation, to the exclusion of other determinants of speciation rate. In cases of closely related clades that differ in diversity by orders of magnitude, as just noted, it is likely that they all had the same original modes of reproductive isolation, so other factors must have determined their subsequent massively different evolutionary trajectories. These other factors include the innate rate of splitting within a clade, and population persistence in which incipient species avoid demographic extinction.

Liow & Finarelli (2016) continue on the theme of taxonomic diversification with a detailed study of the past 28 million years of northern hemisphere carnivoran mammal diversification, using an extensive dataset of fossil occurrences extracted from the Paleobiology Database (https://www.paleobiodb.org). They borrow from sampling strategies utilized by ecological research, applying a capture-mark-recapture approach to ameliorate biases in our sampling of the fossil record. Whereas their total dataset ('global') analysis recovered a relatively stable net diversification, their results demonstrate geographical variation, especially in the late Neogene. A peak in positive diversification is restricted to Eurasia 9–8 Ma, and coincides with large-scale vegetation changes that dramatically altered the regional climate. Similar vegetational changes in North America did not occur until a few million years later. In contrast, 6–5 Ma, North American carnivorans showed a positive diversification peak, whilst their Eurasian counterparts suffered negative diversification, coinciding with the Messinian Salinity Crisis. With the exception of Caniformia (the group that includes dogs and bears), which has lower speciation rates in North America than in Europe, net rates of diversification do not differ between other carnivoran subclades, nor between the two regions. Liow & Finarelli's (2016) study adds to the growing body of literature demonstrating the importance of examining regional, as well as global, patterns of palaeodiversity.

Modelling trait evolution

Clades evolve not just in numbers, but also in form, and macroevolutionary analyses of the evolution of traits have benefited greatly from developments in image data collection, morphometrics, and phylogenetic comparative methods to reconstruct clade dynamics from the perspective of morphological evolution and disparification (e.g. Adams et al., 2013; Brusatte et al., 2008; Drake & Klingenberg, 2010; Harmon et al., 2010; Jones et al., 2015;

Polly, 2004). Similar to Liow & Finarelli (2016), Polly et al. (2016) focus on the local processes that can have a dramatic effect on organismal evolution. Rather than taxonomic diversity, however, they examine morphological evolution, simulating the role of these smaller-scale processes in shaping clade dynamics through the lens of ecometric patterning, a means to describe and analyse ways in which organisms track changing physical environments. Their analysis is performed at the community level, recording how species within a community track optimal environmental conditions, either by adapting through natural selection, diversifying through speciation or succumbing to extinction. The physical environment has a direct impact on species through factors such as ambient temperature, oxygen concentration, physical topography, predator abundance, and food quality. Species can respond to these varying drivers through their integument cover, gas exchange surfaces, locomotor morphology, and masticatory mechanics. The authors explore the evolution of hypsodonty, the elongation of the molar teeth, in various plant-eating mammals through the Cenozoic, and test their data against numerous possible models. They find that phylogenetic structuring arose only when selection intensity, dispersal, and extirpation were all high. Ancestry and environmental geography produced historical effects on patterns of trait evolution and local diversity of species, but ecometric patterns appeared to be largely deterministic. Phylogenetic trait correlations and clade sorting appeared to arise more easily in changing environments than static ones. Microevolutionary parameters and historical factors both affected ecometric lag time and thus the balance between extinction, adaptation, and geographic reorganization as responses to climate change.

Simulations provide a powerful approach to reconstructing complex effects and generating hypotheses that can be tested with empirical data (e.g. Goswami et al., 2014; Hunt, 2012; Polly, 2004; Slater et al., 2012; Wagner, 2000). As the studies in this volume demonstrate, the field of macroevolutionary research and the use of phylogenetic comparative methods have experienced vast growth in recent years. A large part of this increase may be attributed to the increasing availability of free software and code for running complex macroevolutionary analyses, which has been, and should be, lauded. Indeed, many of the studies in this volume describe new approaches, and provide the necessary code to run those methods, precisely to further expand the field of macroevolutionary analysis. However, with great analytical power comes great analytical responsibility, as Cooper et al.

(2016) discuss in their contribution. Most methods for reconstructing trait evolution are based on Brownian motion models, which assume that trait variance is a function of time (e.g., branch length) and thus that similarity in form reflects closeness of relationship. Several expansions of this basic model have been developed over many years, including single and multiple Ornstein--Uhlenbeck (OU) models and adaptive peak models, in which traits are drawn to certain optimal values rather than evolving randomly. Cooper et al. (2016) focus in particular on the use (and misuse) of OU models, simulating many common scenarios in which OU models are incorrectly preferred over simpler models. Of particular note is the sensitivity of this issue to measurement error and small tree size (and small is relative – they mean trees with fewer than 1000 tips). As OU models have become a regular inclusion in macroevolutionary analyses, implemented in many common analytical packages, and as new multi-OU models will only exacerbate these issues by essentially splitting effective tree size with each additional peak, Cooper et al. (2016) make a strong argument for caution in the application of these methods without full consideration of their weaknesses, and they provide a useful list of recommendations to guard again misapplication and misinterpretation of OU models.

Smaers et al. (2016) expand on our current toolkit for reconstructing trait evolution by describing a new adaptive-peak-based model for phylogenetic comparative analysis in which rates of evolution may vary on different branches. They note that most current formulations use the Brownian motion (BM) model as the null, in which the rate of evolution is stochastically constant across all branches, and that the average trait change is proportional to the square root of time. These assumptions, however, differ from the common view that different traits may evolve at different rates, and those rates may differ between subclades in a tree. In their new model, Smaers et al. (2016) allow evolutionary rates to differ along different branches of the phylogenetic tree, and they provide a multiple variance BM model as the null. In simulations, they show that their model can replicate results for a constant variance BM, and that in cases where rates vary along different branches, their model outperforms the traditional model. In an empirical study of the evolution of the primate brain and body mass, their model provides an improved statistical fit relative to other methods, and estimates of nodal values lie within the expected range based on the fossil record.

Baker et al. (2016) continue along this theme of variable rates in presenting a new approach for detecting exceptional shifts in the rate of phenotypic evolution, without the requirement of genetic data. Positive phenotypic selection is recognized where variation in the rate of morphological evolution is at least twice that of the background rate, and the authors suggest that this is widespread and common in nature, demonstrating its presence in a wide range of organisms, including *Anolis* lizards, paravian (bird-line) dinosaurs, mammals (cetaceans and primates), and fleshy fruit angiosperms. Based on these findings from a diverse sample of extant and extinct life, Baker et al. (2016) argue that episodic, rather than gradual, patterns in phenotypic macroevolution are the norm, dovetailing with the view from genetic studies, and indicating that analyses using simplistic evolutionary models based on homogeneous rates are likely to produce misleading results. Lastly, by enabling the recognition of rate heterogeneity without recourse to genetic data, Baker et al.'s (2016) approach allows the detection of deep time patterns of natural selection in taxa known only from fossils.

Measuring morphological diversity

Trait evolution is of course the precursor to diversification of form, and studies of morphological diversity can provide a novel perspective from both taxonomic diversity and evolutionary rate. While all of these attributes may be aligned in certain scenarios, such as adaptive radiations, there are many cases in which evolutionary rates and disparity, or taxonomic diversity and disparity (e.g. Foote, 1993; Ruta et al., 2013), may be discordant. Measuring morphological disparity can take many forms, from univariate or multivariate continuous traits to discrete, or cladistics, traits. Each approach has its strengths and weaknesses, in terms of comparability, sensitivity to missing data (as is common with palaeontological datasets), and representation of organismal form, and all provide important information on how organisms diversify under different conditions (Foote, 1997). The following three papers approach the topic of morphological disparity with discrete character data, such as those commonly gathered for morphological phylogenetic analyses, providing an overview of measuring overall disparity as well as an extension for examining trends in disparity, detailed description and code for analyses of morphological disparity,

and a worked example focused on the archetypal adaptive radiation, the placental mammals after the end-Cretaceous mass extinction, 66 million years ago.

As discussed in Hopkins (2016), there has been considerable work on morphological disparity using morphospaces to visualize changes in disparity through time, as well as quantifying these changes with metrics such as mean pairwise dissimilarity or overall morphospace occupation. However, she points out that directionality is frequently overlooked in studies of disparity, despite being the more emphasized aspect in studies of macroevolutionary trends. In this contribution, Hopkins (2016) analyses trends in morphological evolution in post-Palaeozoic echinoids and Cambrian pterocephaliid trilobites and demonstrates how observed trends within specific subclades can shape morphological disparity across clades. Long-term biases in both the direction of morphological evolution and the magnitude of change are observed to increase disparity through time in more inclusive clades, but not necessarily in the subclades exhibiting these trends. Increases in disparity in a large clade may also result from passive diffusion, or a combination of passive diffusion and active trends in only a small proportion of lineages or subclades. Thus, Hopkins (2016) demonstrates that understanding the mechanisms underlying morphological diversification benefits from examining directionality in morphological change, and not just its magnitude.

Lloyd (2016) continues on the topic of morphological disparity, as well as rate, as measured in a phylogenetic context using cladistic (i.e., discrete) character data. Cladistic data offer many advantages for large-scale analyses of morphological evolution, as they are routinely gathered for phylogenetic analyses, usually attempt to maximize coverage of the organism's anatomy, and often are more comparable across very large clades than are morphometric data. They also benefit from having associated phylogenetic trees, which are important for many methods of macroevolutionary analysis. Lloyd (2016) provides a thoughtful, comprehensive, and practical guide to conducting analyses of disparity and evolutionary rate using cladistic data, as well as introducing a new R package *Claddis* that can perform many of the described analyses. He conducts simulations to demonstrate which metrics are most accurate, as well as developing a new, and potentially better, distance metric for analyses of cladistic data. As these fields grow, and discrete character datasets become

increasingly available (due to the existing norm of publishing datasets for phylogenetic analyses), the useful discussion of issues such as time-scaling of trees, effects of missing data, and approaches to ordination, is important for researchers new to this field, as well as those who have been part of its development over the last few decades.

Finally, Halliday & Goswami (2016) return to the topic of adaptive radiations, and the significance of dramatic global events in shaping diversity. Employing the approaches discussed in Lloyd (2016), they assess phylogenetic measures of morphological disparity in Cretaceous–Paleocene eutherian mammals and provide support for a placental mammal adaptive radiation after the end-Cretaceous mass extinction (66 million years ago). Utilizing an extensive phylogenetic data matrix of fossil eutherian taxa, including heavy sampling of Cretaceous and Palaeogene taxa, coupled with reconstructions of ancestral morphologies for all characters and nodes, these authors used the resultant distance matrix to calculate morphological range- and variance-based disparity. In the last two stratigraphic stages of the Cretaceous, Halliday & Goswami (2016) document an increase in total morphospace occupation from the Campanian to the Maastrichtian, but a decrease in average dissimilarity among taxa. They interpret this as corresponding to a faunal turnover, whereby basal eutherians were replaced by taxa closer to the placental radiation. Morphospace range increases most strikingly immediately after the mass extinction, although mean dissimilarity lags behind, suggesting an adaptive radiation followed by later ecological specialisations that resulted in increased dissimilarity through the early Palaeogene. Thus, this study provides substantial support that, while some changes in the eutherian fauna began in the Late Cretaceous, the Cretaceous/Palaeogene mass extinction had a dramatic effect on the evolution of eutherian mammals and led to an adaptive radiation of placental mammals.

Conclusions

The past few decades have represented a step-change in macroevolutionary research. New approaches and new sources of data in macroevolution and macroecology have enabled researchers to conduct robust quantitative tests of many long-standing debates in the evolution of biodiversity, and have also introduced new debates on methodological choices and important limitations of data and sampling. The current set of papers represents these

massive changes in the study of clade dynamics through deep time. The authors in this special volume explore speciation, trait evolution, and morphological diversity, core components of any macroevolutionary study. They provide critical analyses of existing methods, descriptions and worked examples of new methods, and novel applications of approaches borrowed from other fields of research. The result is a volume that covers topics that are fundamental to macroevolutionary research and provides useful guides on analytical methods for new entrants to the field, as well as for seasoned veterans. We fully expect that this rapid progress in macroevolutionary research will persist well into the future, and we hope that this special issue will serve as a valuable resource for the next generation of macroevolutionary biologists as they continue to improve on the work presented here.

Acknowledgements

We are grateful to the Linnean Society of London for hosting the symposium that resulted in this volume and to Imperial College London for hosting the workshop associated with the symposium. In particular, Tom Simpson of the Linnean Society provided extensive logistical support for the meeting. We further thank the Linnean Society of London, the Palaeontological Association, and University College London for financial support of this meeting and workshop, and we thank all of the contributors and attendees for the rich discussion that inspired this volume.

References

Adams DC, Rohlf FJ, Slice DE. 2013. A field comes of age: geometric morphometrics in the 21st century. *Hystrix* **24:** 7-14.

Alfaro ME, Santini F, Brock C, Alamillo H, Dornburg A, Rabosky DL, Carnevale G, Harmon LJ. 2009. Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. *Proceedings of the National Academy of Sciences of the United States of America* **108:** 6187-6192.

Alroy J. 1999. The fossil record of North American mammals: evidence for a Paleocene evolutionary radiation. *Systematic Biology* **48:** 107-118.

Aze T, Ezard THG, Purvis A, Coxall HK, Stewart DRM, Wade BS, Pearson PN. 2011. A phylogeny of Cenozoic macroperforate planktonic foraminifera from fossil data. *Biological Reviews* **86:** 900-927.

Baker J, Meade A, Pagel M, Venditti C. 2016. Positive phenotypic selection inferred from phylogenies. *Biological Journal of the Linnean Society* **in press**.

Bininda-Emonds ORP, Gittleman JL, Purvis A. 1999. Building large trees by combining phylogenetic information: a complete phylogeny of the extant Carnivora (Mammalia). *Biological Reviews* **74:** 143-175.

Bown TM, Holroyd PA, Rose KD. 1994. Mammal Extinctions, Body-Size, and Paleotemperature. *Proceedings of the National Academy of Sciences of the United States of America* **91:** 10403-10406.

Brown RP, Yang Z. 2011. Rate variation and estimation of divergence times using strict and relaxed clocks. *BMC Evolutionary Biology* **in press**.

Brusatte SL, Benton MJ, Ruta M, Lloyd GT. 2008. The first 50Myr of dinosaur evolution: macroevolutionary pattern and morphological disparity. *Biology Letters* **4:** 733-736.

Cooper N, Thomas GH, Venditti C, Meade A, Freckleton RP. 2016. A cautionary note on the use of Ornstein Uhlenbeck models in macroevolutionary studies. *Biological Journal of the Linnean Society* **in press**.

Cuvier G. 1825. *On the revolutions of the surface of the globe, and the changes thereby produced in the animal kingdom*. G. Dufour et Ed. D'Ocagne: Paris.

Darwin C. 1859. *The origin of species*. John Murray: London.

Donoghue PCJ, Benton MJ. 2007. Rocks and clocks: calibrating the Tree of Life using fossils and molecules. *Trends in Ecology & Evolution* **22:** 424-431.

dos Reis M, Inoue J, Hasegawa M, Asher RJ, Donoghue PCJ, Yang Z. 2012. Phylogenomic datasets provide both precision and accuracy in estimating the timescale of placental mammal phylogeny. *Proceedings of the Royal Society B* **279:** 3491-3500.

Drake AG, Klingenberg CP. 2010. Large-scale diversification of skull shape in domestic dogs: disparity and modularity. *American Naturalist* **175:** 289-301.

Finarelli JA, Goswami A. 2013. Potential pitfalls of reconstructing deep time evolutionary history with only extant data, a case study using the Canidae. *Evolution* **67:** 3678-3685.

Foote M. 1993. Discordance and concordance between morphological and taxonomic diversity. *Paleobiology* **19:** 185-204.

Foote M. 1997. The evoution of morphological diversity. *Annual Review of Ecology and Systematics* **28:** 129-152.

Goswami A, Smaers JB, Soligo C, Polly PD. 2014. The macroevolutionary consequences of phenotypic integration: from development to deep time. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* **369:** 20130254.

Halliday TJD, Goswami A. 2016. Eutherian morphological disparity across the end-Cretaceous mass extinction. *Biological Journal of the Linnean Society* **in press**.

Harmon LJ, Losos JB, Davies TJ, Gillespie RG, Gittleman JL, Jennings WB, Kozak KH. 2010. Early bursts of body size and shape evolution are rare in comparative data. *Evolution* **64:** 2385-2396.

Hopkins MJ. 2016. Magnitude vs direction of change and the contribution of macroevolutionary trends to morphological disparity. *Biological Journal of the Linnean Society* **in press**.

Hunt G. 2007. The relative importance of directional change, random walks, and stasis in the evolution of fossil lineages. *Proceedings of the National Academy of Sciences of the United States of America* **104:** 18404-18408.

Hunt G. 2012. Measuring rates of phenotypic evolution and the inseparability of tempo and mode. *Paleobiology* **38:** 351-373.

Jablonski D. 2001. Lessons from the past: evolutionary impacts of mass extinctions. *Proceedings of the National Academy of Sciences of the United States of America* **98:** 5393-5398.

Jablonski D, Chaloner WG. 1994. EXTINCTIONS IN THE FOSSIL RECORD. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences* **344:** 11-16.

Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO. 2012. The global diversity of birds in space and time. *Nature* **491:** 444-448.

Jones KE, Smaers JB, Goswami A. 2015. Impact of the terrestrial-aquatic transition on disparity and rates of evolution in the carnivoran skull. *BMC Evolutionary Biology* **15:** 8.

Lloyd GT. 2016. Estimating morphological diversity and tempo with discrete character-taxon matrices: implementation, challenges, progress, and future directions. *Biological Journal of the Linnean Society* **in press**.

Losos JB. 2010. Adaptive radiation, ecological opportunity, and evolutionary determinism. *American Naturalist* **175:** 623-639.

Meredith RW, Janecka JE, Gatesy J, Ryder OA, Fisher CA, Teeling EC, Goodbla A, Eizirik E, Simao TLL, Stadler T, Rabosky DL, Honeycutt RL, Flynn JJ, Ingram CM, Steiner C, Williams TL, Robinson TJ, Burk-Herrick A, Westerman M, Ayoub NA, Springer MS, Murphy WJ. 2011. Impacts of the Cretaceous Terrestrial Revolution and KPg Extinction on Mammal Diversification. *Science* **334:** 521-524.

Polly PD. 2004. On the simulation of the evolution of morphological shape: multivariate shape under selection and drift. *Palaeontologia Electronica* **7.2.7A:** 1-28.

Polly PD, Lawing AM, Eronen JT, Schnitzler J. 2016. Processes of ecometric patterning: modelling functional traits, environments, and clade dynamics in deep time. *Biological Journal of the Linnean Society* **in press**.

Rabosky DL. 2016. Reproductive isolation and the causes of speciation rate variation in nature. *Biological Journal of the Linnean Society* **in press**.

Raup DM, Sepkoski JJ. 1982. Mass extinctions in the marine fossil record. *Science* **215:** 1501-1503.

Ruta M, Angielczyk KD, Froebisch J, Benton MJ. 2013. Decoupling of morphological disparity and taxic diversity during the adaptive radiation of anomodonts. *Proceedings of the Royal Society of London, Series B: Biological Sciences* **280:** 1768-1778.

Simpson GG. 1944. *Tempo and mode in evolution*. Columbia Univ. Press: New York.

Slater GJ, Harmon LJ, Alfaro ME. 2012. Integating fossils with molecular phylogenies improves inference of trait evolution. *Evolution* **66:** 3931-3944.

Smaers JB, Mongle CS, Kandler A. 2016. A multiple variance Brownian motion framework for estimating variable rates and inferring ancestral states. *Biological Journal of the Linnean Society* **in press**.

Stadler T. 2011. Mammalian phylogeny reveals recent diversification rate shifts. *Proceedings of the National Academy of Sciences of the United States of America* **108:** 6187-6192.

Wagner PJ. 2000. The quality of the fossil record and the accuracy of phylogenetic inferences about sampling and diversity. *Systematic Biology* **49:** 65-86.

Wiens JJ, Kuczynski CA, Townsend T, Reeder TW, Mulcahy DG, J.W. Sites J. 2010. Combining phylogenomics and fossils in higher-level squamate reptile phylogeny: molecular data change the placement of fossil taxa. *Systematic Biology* **59:** 674-688.

Yang Z, Rannala B. 2006. Bayesian estimation of species divergence times under a molecular clock using multiple fossil calibrations with soft bounds. *Molecular Biology and Evolution* **23:** 212-226.

Zachos J, Pagani M, Sloan L, Thomas E, Billups K. 2001. Trends, rhythms, and abberations in global climate 65 Ma to present. *Science* **292:** 686-693.